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Enhancing cognitive control through neurofeedback: A role of gamma-band activity in managing episodic retrieval

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ABSTRACT

Neural synchronization has been proposed to be the underlying mechanism for exchanging and integrating anatomically distributed information and has been associated with a myriad of cognitive domains, including visual feature binding, top–down control, and long-term memory. Moreover, it seems that separate frequency bands have different functions in these cognitive processes. Here we studied whether neurofeedback training designed either to increase local gamma band activity (GBA+; 36–44 Hz), or local beta band activity (BBA+; 12–20 Hz), would have an impact on performance of behavioral tasks measuring short-term and long-term episodic binding. Our results show that GBA-enhancing neurofeedback training increased occipital GBA within sessions, and occipital and frontal GBA across sessions. Both groups showed an increase of GBA coherence between frontal and occipital areas, but the BBA+ group increased BBA coherence between these areas as well. Neurofeedback training had profound effects on behavior. First, we replicated earlier findings that enhancing GBA led to greater flexibility in handling (selectively retrieving) episodic bindings, which points to a role of GBA in top–down control of memory retrieval. Moreover, the long-term memory task revealed a double dissociation: GBA-targeted training improved recollection, whereas BBA-targeted training improved familiarity memory. We conclude that GBA is important for controlling and organizing memory traces of relational information in both short-term binding and long-term memory, while frontal–occipital coherence in the beta band may facilitate familiarity processes.

Introduction

The primate brain, and the human brain in particular, is divided into modules that are (often highly) specialized in processing particular information (e.g., Kourtzi and Kanwisher, 2000; Zeki et al., 1991; Treisman, 1996). This renders communication about, exchange, and integration of distributed information a vital function of human cognition, and poses the question of how neural communication is organized. A possible mechanism underlying this function is the temporal synchronization of neural firing rates (e.g., Singer, 1999; Von der Malsburg, 1999). Neural synchronization has been assumed to play a crucial role in the integration of visual features (for an overview, see Engel and Singer, 2001; Jensen et al., 2007), intermodal integration (Von Stein et al., 1999), and visuomotor integration (Roelfsema et al., 1997), but also in attentional selection (Fell et al., 2003), short-term memory retention (Tallon-Baudry and Bertrand, 1999), long-term memory (Klimesch, 1999), and visual awareness (Engel and Singer, 2001). It has been proposed that communication between brain areas may rely on increasingly lower frequency bands as the distance between brain areas increases (Varela et al., 2001). More specifically, it has been suggested that neural firings in the gamma range (~30–100 Hz) are related to local feature integration and short-term memory (e.g., Tallon-Baudry and Bertrand, 1999), whereas larger anatomical distances are bridged by beta band activity (BBA; ~12–20 Hz), such as in intermodal integration (Von Stein et al., 1999), visuomotor processing (Roelfsema et al., 1997), or the transfer of frontal control signals to parietal and occipital areas (Gross et al., 2004, 2006). In the literature the term neural synchrony is used rather loosely, since it can refer to both local synchrony and long-range synchrony. However, in the context of EEG research it is important to distinguish between these two. Local synchrony refers to the synchronous firing of neurons within a particular brain area, whereas long-range synchrony can be described as synchronous firing of groups of neurons in different, spatially distinct brain areas. In EEG research, local synchrony is assumed to be reflected by the power of a particular frequency band at a particular electrode site, while long-range synchrony is taken to be reflected by the coherence between two (distal) electrode sites within a particular frequency band and is usually associated with the amount of communication between two brain areas (Bressler et al., 1993; Varela et al., 2001).

Even though an increasing amount of studies report correlations between neural synchronization and cognitive processing, the functional relevance of neural synchronization is still under heavy debate (Ghose and Maunsell, 1999; Reynolds and Desimone, 1999;

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Shadlen and Movshon, 1999; Treisman, 1999). One of the reasons for this debate is that demonstrations of correlations between neural synchrony and cognitive processes cannot rule out that neural synchrony is epiphenomenal to cognitive functions. In order to investigate whether neural synchrony is functionally relevant for cognitive processes, studies in which neural synchrony is treated as an independent variable instead of a dependent variable are needed. In other words, when experimental manipulation of neural synchrony has an impact on behavioral measures of integration, top–down control or memory, inferences can be made about the causal role of neural synchrony in the mechanisms that underlie these different cognitive domains.

A first step in this endeavor would be to show that impairment of neural synchrony leads to decreased performance on tasks that measure cognitive processes for which neural synchrony is presumably important. Indeed, studies have shown patients suffering from schizophrenia show decreased neural synchronization (for an overview, see Uhlhaas et al., 2008), including GBA (for an overview, see Lee et al., 2003). In a recent study by Spencer et al. (2004) it was shown that the abnormalities of GBA in schizophrenia are related to poor performance on tasks that required integration of visual information. Interestingly, 'disintegration' of personality and thoughts is generally regarded as the core symptom of schizophrenia (Spencer et al., 2004). Indeed, the study of Spencer et al. (2004) showed that the severity of the schizophrenia-related symptoms correlates with the poor performance on a visual binding task.

However, studying the effects of neurological impairments on cognition has a number of well-known drawbacks. First, neurological diseases seldom affect neural synchrony selectively and second, patients may have adopted compensatory strategies to cope with their impairments. Moreover, (a history of) medication use may also affect the cognitive processes under investigation. In addition to studies on neurological disorders, studies are needed that manipulate neural synchrony in a more direct way in order to infer causal roles to neural synchrony. In previous research, several methods have been used to manipulate neural synchrony in more direct ways, such as psycho-active drugs (Rodriguez-Bermudez et al., 2004), visual flicker stimuli (Bauer et al., 2009), and repetitive transcranial magnetic stimulation (rTMS; Thut and Miniussi, 2009). For instance, it has been demonstrated that muscarinic–cholinergic agonists enhance both GBA (Rodriguez-Bermudez et al., 2004) and the binding of visual features (Colzato et al., 2005), whereas muscarinic–cholinergic antagonists impair GBA (Rodriguez-Bermudez et al., 2004) and visual integration (Colzato et al., 2004). Other studies have shown that flickering visual stimuli entrain neural activity in the visual cortex and can facilitate cognitive processes, especially with flicker rates in the gamma-range (50-Hz; e.g., Bauer et al., 2009). Finally, rTMS has been shown to influence neural synchrony in the alpha band (8–14 Hz) and the beta band (14–30 Hz; e.g. Strens et al., 2002; Tamura et al., 2005; Thut et al., 2003).

In the present study, we used neurofeedback to see whether the experimental manipulation of neural synchrony can be demonstrated to lead to systematic changes in cognitive processes. Even though it is true that the widespread advertisement and application of neurofeedback methods in clinical domains is not always based on firm scientific grounds, there is reliable evidence that local synchrony can be systematically enhanced or reduced by neurofeedback methods (Bird et al., 1978; Vernon et al., 2003). With neurofeedback training, an online spectrum analysis is performed on the EEG signal that is measured from electrodes attached to the subject's scalp. Providing subjects with real-time feedback regarding the power of a particular frequency band makes it possible for the subject to systematically alter the targeted frequency band(s), at least in some cases.

A few studies have studied the relationship between local synchrony and cognitive functions as a function of neurofeedback in healthy subjects. Vernon et al. (2003) showed that providing feedback about BBA recorded from the sensorimotor cortex allowed participants to increase performance on a semantic visual short-term memory task. Recent findings from our lab suggest that enhancing local GBA with neurofeedback training affects the way people deal with episodic feature bindings (Keizer et al., in press). Our results show that subjects who enhanced their GBA on an occipital electrode site were more flexible in handling bindings between two features of visual objects, their shape and location. Changes in GBA also correlated positively with changes in fluid intelligence from pretest to posttest, as measured with Raven's standard progressive matrices (Raven, 1938). This correlation is in accordance with the finding that subjects with a high fluid intelligence show more flexibility in handling visually integrated information (Colzato et al., 2006) and that GBA and fluid intelligence may be related (Jausovec, 2004, Jausovec and Jausovec, 2005, 2007; Stankov et al., 2006). Since fluid intelligence is arguably related to cognitive control (Kane and Engle, 2002), it can be argued that GBA-targeted neurofeedback may not so much enhance the mechanism underlying the actual integration of information but more the efficiency with which integrated information (episodic memory traces) is organized and controlled. If so, enhancing occipital GBA by means of neurofeedback would be a way to enhance cognitive control, and the control of episodic memory retrieval in particular.

To provide more specific evidence to support this idea, we extended our previous neurofeedback study on feature binding (Keizer et al., in press) in several ways. First, we increased the number of electrodes used in the neurofeedback sessions. In our previous study we employed one occipital electrode (Oz) to measure the effect of GBA-enhancing neurofeedback on visual processing. Our original idea was that GBA-targeted neurofeedback might enhance local processes subserving visual binding, so that the visual cortex was an obvious choice. However, as already pointed out, the findings of Keizer et al., (in press) suggest that enhancing occipital GBA improves cognitive-control processes, which might affect the visual cortex but are unlikely to have their origin there. Accordingly, we used two electrodes in the current study, one occipital electrode (Oz) and one frontal electrode (Fz). The latter would allow us to monitor local synchrony in frontal brain regions, but also to study the effects of neurofeedback on coherence between occipital and frontal sites. In contrast to GBA, BBA has been assumed to subserve communication between anatomically remote areas (e.g., Schnitzler et al., 2000) and/or the integration of visual and motor features (Colzato et al., 2007), so that we based BBA-related neurofeedback on both the occipital and the frontal electrode. That is, the feedback was aimed to enhance BBA at Oz and Fz. It can be hypothesized that enhancing BBA on both frontal and occipital sites would facilitate communication between these two, which may also be reflected in BBA coherence between Oz and Fz.

A second change with respect to our previous method relates to the criterion for providing neurofeedback. In our previous study, subjects received feedback that was aimed to increase either GBA or BBA at the occipital electrode. The 'GBA+' group successfully enhanced GBA on the occipital electrode from the first to the last neurofeedback session, whereas no significant changes were obtained for the 'BBA+' group. One reason for the absence of any effect on occipital BBA may be that subjects received neurofeedback according to a criterion that coupled the two frequency bands, that is, neurofeedback was provided so to increase BBA and reduce GBA at the same time. This dual criterion may have been too difficult to achieve, so that we in the present study provided feedback with respect to the targeted frequency band only. For GBA+, the occipital electrode again served as feedback criteria, that is, the feedback was aimed to enhance GBA at the Oz electrode. For BBA+, feedback was aimed to enhance BBA at the occipital and frontal electrodes.

Finally, we extended our behavioral tests to an episodic long-term memory (LTM) task. As pointed out already, our previous study suggested that GBA neurofeedback may improve the control of retrieval of episodic memory bindings. However, the task we used was tailored to assess the retrieval of implicitly created, task-irrelevant, and only briefly maintained feature conjunctions, so that we were interested to see whether our observations would extend to a more standard episodic memory task with longer retention intervals. A larger body of research indeed suggests that neural synchrony may play a role in LTM (Klimesch, 1999; Sederberg et al., 2003). For instance, Sederberg et al. (2003) showed that the probability of subsequent recall is predicted by the amount of GBA that occurs during encoding. It has also been suggested that the role of GBA is to match sensory information with representations stored in LTM (Herrmann et al., 2004; Hermann et al., 2004), which would point to the importance of GBA for retrieval. This is in accordance with findings of Burgess and Ali (2002), who studied GBA during recognition of visual information stored in LTM. They used a version of the remember/know paradigm, which distinguishes between two subjective states of correct recognition: 'recollection' and 'familiarity'. Recollection refers to the conscious recognition of an event, including contextual information, whereas familiarity refers to weaker recognition—a sense of familiarity without access to contextual information. The results of Burgess and Ali (2002) showed that the subjective experience of recollection was associated with more GBA than the subjective experience of familiarity. Interestingly, recollection was also related with greater functional connectivity in the gamma range than familiarity.

In addition to GBA, many studies also show that theta band activity (TBA; 4–8 Hz) is related with LTM processes (for an overview, see Klimesch, 1999). It has been suggested that GBA and TBA play complementary roles in LTM (Lisman and Buzsáki, 2008), which is supported by the finding that show 'entrainment' of GBA by TBA (Sirota et al., 2008). Even though both GBA and TBA predict successful retrieval of information stored in LTM, the results of a recent study by Gruber et al. (2008) suggests that GBA and TBA have dissociable functions in LTM. Gruber et al. (2008) used a source memory task, where familiarity corresponded with the ability to judge whether an item presented in the retrieval phase was also presented in the encoding phase and recollection corresponded with the ability to retrieve information in the retrieval phase that was combined with an item during the encoding phase but not during the retrieval phase. Results showed that occipital/parietal GBA was related to familiarity and frontal TBA was related to recollection. Even though altering TBA with neurofeedback has been demonstrated in previous research using healthy subjects (Egner and Gruzelier, 2003), we have currently not been able to replicate these effects in our lab. Therefore, we chose to focus on GBA and BBA in the present study. To summarize, research on LTM suggests a functional role of GBA but is ambiguous regarding the processes GBA may support. On the one hand, research suggests that GBA is important for recollection but not for familiarity (Burgess and Ali, 2002). On the other hand, the findings of Gruber et al. (2008) suggest that GBA is important for familiarity, but not for recollection. To look into this issue we included a LTM-memory task that could distinguish between recognition and familiarity.

Method

Participants

17 right-handed volunteers (2 male, mean age: 22.6 years) participated in the experiment. Informed consent was obtained from all participants after the nature and possible consequences of the study were explained to them. The protocol was approved by the local medical ethical committee (Leiden University Medical Center).

Procedure

Each subject was randomly assigned to one of the two groups (eight in the GBA+ group and nine in the BBA+). In a double-blind procedure, both the subject and the experimenter were unaware which of the two possible neurofeedback training protocols was given to the subject until the last subject completed the experiment. Subjects filled out a questionnaire before the start of each neurofeedback training session, enquiring for any notable changes in appetite, sleep pattern, ability to concentrate, memory capacity, and mood. The order of the behavioral tests (binding and long-term memory) was counterbalanced across subjects.

Neurofeedback training

Fifteen subjects completed 8, and two subjects completed 7 neurofeedback sessions. There was one 30-min training session per day. The neurofeedback sessions were spread over a period of 10 or 11 days. For the EEG measurements, a QDS Focus amplifier and electrodes were used (www.brain-trainer.com). The EEG signal was received from two electrodes attached to the scalp of the subject, one on the Oz position and one on the Fz position, according to the international 10–20 system. Reference electrodes were placed on both earlobes and forehead of the subject. Electrode impedances were kept below 10 kΩ. The EEG power spectrum analysis was calculated online with negligible delay, using the Bioexplorer software package (www.cyberrevolution.com). An elliptic filter was applied to the signal, extracting frequencies from the Oz electrode in the gamma range (36–44 Hz) for the GBA+ group and from the Oz and Fz electrodes in the Beta range (12–20 Hz). An 'upper' threshold was implemented for both groups that was adapting to the power of the frequency band it was applied to. More specifically, the power level was based on a moving average of 30 s that was updated continuously with the average power that was calculated over epochs of 0.125 s and the thresholds were set to the power level that would be surpassed 75% of the time during the preceding 30 second window. Even though the gamma band has been defined in the range of 30 and 100 Hz, we chose to operationalize the gamma band around 40 Hz, since this seems to be the most widely accepted and most referred to indicator of the gamma band in humans (i.e. Tallon-Baudry and Bertrand, 1999).

In the GBA+ group, a tone was generated whenever the gamma power of Oz exceeded the upper threshold and in the BBA+ group and a tone was generated whenever the Beta power of both Oz and Fz exceeded the upper threshold. Both groups were instructed to attempt to increase the rate of the tone occurrences. The maximum rate of the tones was set to one tone per second. Using these criteria, subjects achieved a high rate of tones when the power of their frequency bands was recurrently exceeding the adapting thresholds.

Binding

Binding processes were tested by using the exact same task as was used in Keizer et al., (in press), which is a modified version of the task developed by Hommel (1998; see Fig. 1 for an example trial). This task is designed to study the behavioural effects (reaction times and errors) of implicit feature binding. Subjects were instructed to respond with a left or right key press on S1, according to the preceding arrow (3.6° × 2.6°), ignoring the picture (4.8° × 4.1°) and its location (top or bottom). On S2, subjects were instructed to respond to the picture (apple or bananas) while ignoring its location, again with a left or right key press (counterbalanced across subjects). The arrows were presented in the middle square of three equally sized squares (6.0°), placed in vertical alignment, the images of an apple or bananas were placed in either the top or the bottom square. The task consisted of 160 trials, equally divided across conditions.

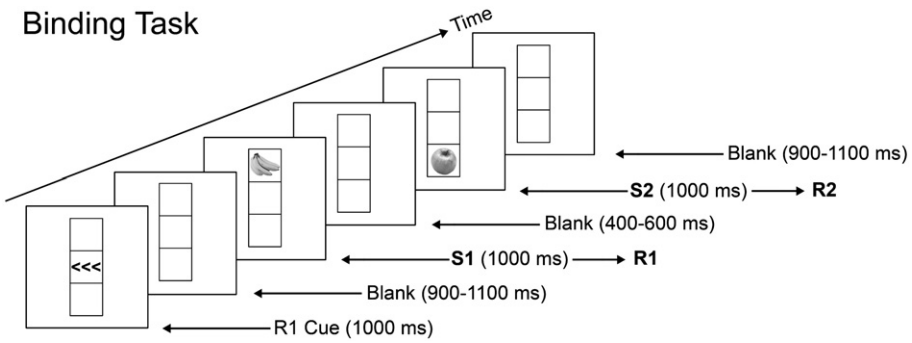

Fig. 1. Time sequence of an example trial in the binding task. Subjects had to respond with a precued response on S1 (according to the preceding arrows) and to the picture of S2 (e.g. bananas–>press left, apple–>press right). Performance costs were measured on the response to S2, in the conditions where features are partially repeated, in comparison with complete repetition or complete alternation of features. It is assumed that the response, picture and location are integrated on S1 and that repeating one, two or all of these features on S2 would automatically reactivate the previously associated features. In the partial repetition conditions, automatic reactivation would lead to inappropriate reactivation of previously associated features, resulting in the performance costs.

The rationale of this design is that on S1, the picture, location and response are integrated into an 'event file' (Hommel, 1998, 2004; Hommel and Colzato, 2004). On S2, the picture, location and response can independently be repeated or alternated. It has been shown in previous studies using a version of this paradigm, that the performance on S2 is impaired when the features of S1 (shape, location, and response) are partially repeated on S2 (Hommel, 1998, 2004; Hommel and Colzato, 2004). The partial-repetition or binding costs can be divided into visual binding costs, which refer the binding between the two visual features (shape and location), and visuomotor binding costs, which refer to the visual features and the action (shape and response, and location and response). Note that binding is not necessary in this task, as the features of S1 are not systematically related to R1, so that integrating S1 and R1 is neither necessary nor helpful. Also of importance, only one of the three possible binary bindings is related to task-relevant feature dimensions. Response location matters for both R1 and R2, and shape matters for selecting S2, whereas stimulus location is nominally irrelevant. Accordingly, only the binding of shape and response relates to task-relevant dimensions, a fact that has been shown to produce stronger and more reliable binding (Hommel, 1998).

Long-term memory

The long-term memory task closely resembled the remember–know paradigm used in the study of Cycowicz et al. (2001). An example trial of

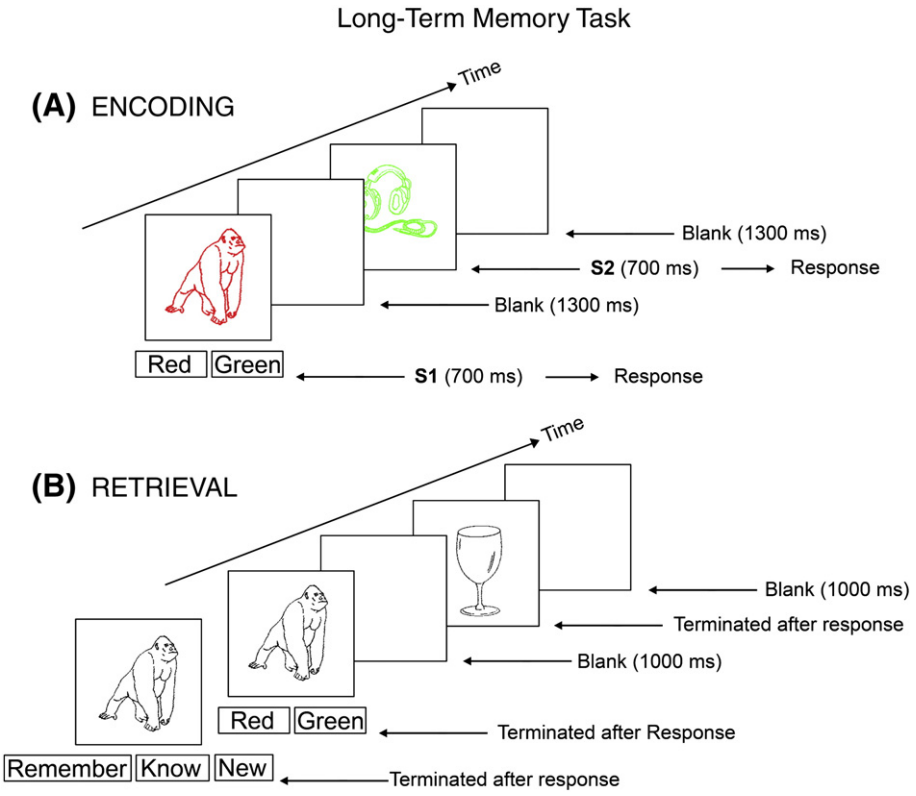

Fig. 2. Time sequence of an example trial of the LTM task in the encoding phase (A) and in the retrieval phase (B). Subjects were instructed to make a color discrimination during the encoding phase. Subjects were told that they should try to remember the occurrence of the drawings and their color, since their memory of the drawings and their color would be tested during the retrieval phase. After the encoding phase was completed, subjects were instructed to make a 'remember–old', 'know–old' or 'new' response on the black-and-white drawings that were presented on the screen. When a subject made either a remember–old or know–old response, the drawing remained on the screen and subjects had to judge whether the drawing was either presented in a red or green color during the encoding phase.

the encoding block and of the retrieval block is shown in Fig. 2. The stimuli consisted of 260 line drawings that were divided into five lists of 52 items each. The lists were constructed in a way that would result in equal judgements of category membership, concept agreement, name agreement, familiarity and visual complexity, according to the normative data bases published in Snodgrass and Vanderwart (1980), Berman et al. (1989) and Cycowicz et al. (1997). There were no significant differences between lists, for all judgements (p's>.15). An additional set of 52 drawings were used for the practice block and fillers. Each subject performed the LTM task four times, two times before the start of the first neurofeedback training and two times after the end of the last neurofeedback training. Four sets of pictures were randomly drawn of the five lists for each subject. The task consisted of 2 phases. Each phase consisted of an encoding block and a retrieval block. For each phase, a different list of drawings was used, the order of which was counterbalanced across subjects. 36 of the drawings in a list (half outlined in green and half in red) were shown in the encoding block, preceded and followed by 2 fillers to avoid primacy and recency effects (subjects were not tested on these fillers). Subjects were instructed to make a discriminative response to the color of the drawing (a left- or right hand response, counterbalanced across subjects) and asked to memorize both the item and the color for the retrieval block.

In the retrieval block 26 black-and-white drawings were presented, 14 new and 12 old (6 that were previously presented in red and 6 in green). Subjects were instructed to judge whether the drawing was 'old-remembered', 'old-know' and 'new', by pressing one of three buttons (left and right index finger and middle finger, counterbalanced across subjects, response options presented below the drawing). This part of the task is believed to tap into recognition memory and has also been used as the 'objective' test of familiarity in the study of Gruber et al. (2008). The distinction between 'remember' and 'know' responses is believed to tap into two distinct conscious states with regard to recognition memory, namely recollection and familiarity (Burgess and Ali, 2002).

If the subjects judged the drawing to be new, the next drawing was presented, after a blank interval of 1000 ms. If a subject judged the drawing to be either old–remembered or old–know, the drawing stayed on the screen and subjects were required to judge whether the drawing was presented in red or green in the encoding phase with a left or right button-press (index fingers, counterbalanced across subjects, response options presented below the drawing). This part of the task has been used as the objective test of recollection in the study of Gruber et al. (2008). After a response was made, the next drawing was presented after a blank interval of 1000 ms.

Results

Questionnaire

No significant group differences were found on any of the items of the questionnaire. Moreover, independent repeated measures ANOVAs showed no significant interactions between group (GBA+ versus BBA+) and test instance (pretest versus posttest) for any of the items of the questionnaire. However, we did find a significant main effect of test instance on the item inquiring subjects to assess their own ability to concentrate, $F(2,15) = 4.9$, $p < .05$, which reflects an increase of the self-assessed ability to concentrate in both groups.

Neurofeedback training

First, we looked into training effects within sessions by comparing the GBA and BBA of the first 5 min and the last 5 min of both the first and the last neurofeedback session. For GBA on Oz, we found a significant three-way interaction between group and the two training factors (within session and between session), $F(2,15) = 11.0$, $p < .005$ (Fig. 3A), and post-hoc comparisons revealed that the GBA+ group

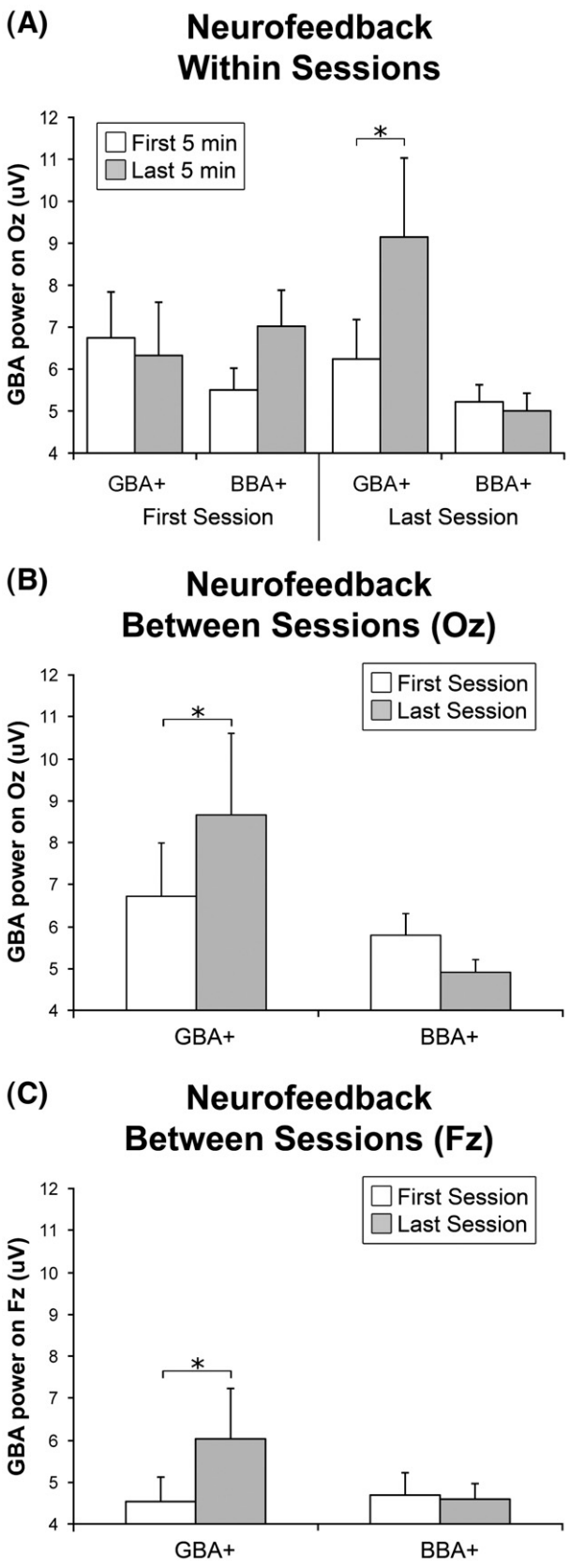

Fig. 3. The neurofeedback training led to an increase of occipital GBA in the GBA+ group compared to the BBA+ group within the last session (first 5 min versus last 5 min) compared with the first session (A). Across sessions (first session versus last session), the neurofeedback training resulted in an increase of occipital (B) and frontal (C) GBA in the GBA+ group compared to the BBA+ group. Error bars represent standard errors, asterisks indicate significance level of $p < .05$.

increased GBA power within the last session, $p<.05$ (first 5 min: 5.0 μV, last 5 min: 9.1 μV). There were no significant effects for GBA on Fz, or BBA on Oz, p's>.06. There was a significant main effect of within session in BBA on Fz, $F(2,15)=5.8$, $p<.05$, which was the result of a within-session increase of BBA in both groups (first 5 min: 10.6 μV, last 5 min: 11.2 μV).

The coherence between Fz and Oz was calculated separately for GBA and BBA. We performed a within-session analyses on the coherence data by comparing the GBA coherence and BBA coherence of the first 5 min and the last 5 min of both the first and the last neurofeedback session. For the GBA coherence, there was a significant two-way interaction between the two training factors (within session and between session), $F(2,15)=5.0$, $p<.05$. Post-hoc comparisons revealed that this interaction was driven by an increase of GBA coherence within the first session for both groups, $p<.05$ (first 5 min: 0.12, last 5 min: 0.15).

Second, we looked at the training effects between sessions by comparing the mean GBA of the first and the last neurofeedback session. Four separate repeated-measures ANOVAs for GBA, BBA, and both electrode positions were performed with GBA or BBA as dependent measure, neurofeedback session (first versus last) as a 2-level within-subjects factors and group (GBA+ or BBA+) as between-subjects factor. First, there was a significant two-way interaction between group and neurofeedback session on the Oz electrode, $F(2, 15)=6.6$, $p<.05$ (Fig. 3B). Post-hoc comparisons showed that this interaction was mainly driven by a significant increase of GBA in the GBA+ group, $p<.05$ (first session: 6.7 μV, last session: 8.7 μV). Second, there was a near-significant two-way interaction between group and neurofeedback session on the Fz electrode, $F(2, 15)=4.3$, $p=.055$ (Fig. 3C). Post-hoc comparisons showed that this interaction was mainly driven by a significant increase of GBA in the GBA+ group, $p<.05$ (first session: 4.5 μV, last session: 6.0 μV). There were no significant interactions between neurofeedback session and group for BBA, p's>.25. We calculated the coherence between Fz and Oz for GBA and BBA separately (Figs. 4A and B). Two separate repeated measures ANOVAs were carried out with either GBA-coherence or BBA-coherence as dependent measure, neurofeedback session (first versus last) as a 2-level within-subjects factors and group (GBA+ or BBA+) as between-subjects factor. A significant main effect of session in GBA-coherence, $F(2,15)=4.7$, $p<.05$, indicated that GBA-coherence increased in both groups from the first session to the last session (Fig. 4A; first session: 0.13, last session: 0.16).

For BBA-coherence, we found a marginally significant main effect of session, $F(2,15)=4.5$, $p=.051$, and a marginally significant interaction between session and group, $F(2,15)=4.5$, $p=.051$. Post-hoc comparisons revealed that these effects were driven by a significant increase of BBA-coherence in the BBA+ group, $p<.01$ (Fig. 4B; first session: 0.12, last session: 0.14).

Binding

Binding effects were assessed by means of repeated measures ANOVAs of reaction times and error rates with repetition versus alternation of stimulus shape, stimulus location, and response as two-level factors and group (GBA+ and BBA+) as a between subjects factor. Reaction times below 200 ms and above 1000 ms were considered as outliers and were discarded (<1% of the data). The pretest showed significant main effects for repetition/alternation of the shape, $F(2,15)=10.4$, $p<.01$, and of the location, $F(2,15)=5.8$, $p<.05$. More importantly, the pretest replicated earlier findings by showing a significant interaction in reaction times between the repetition/alternation of shape and location, $F(2,15)=13.6$, $p<.005$, between the repetition/alternation of location and response, $F(2,15)=57.6$, $p<.000005$ and a marginal significant interaction between the repetition/alternation of shape and response, $F(1,15)=4.5$, $p=.051$. These effects were due to better performance if the features were both repeated or alternated as compared to the repetition of one but not the other.

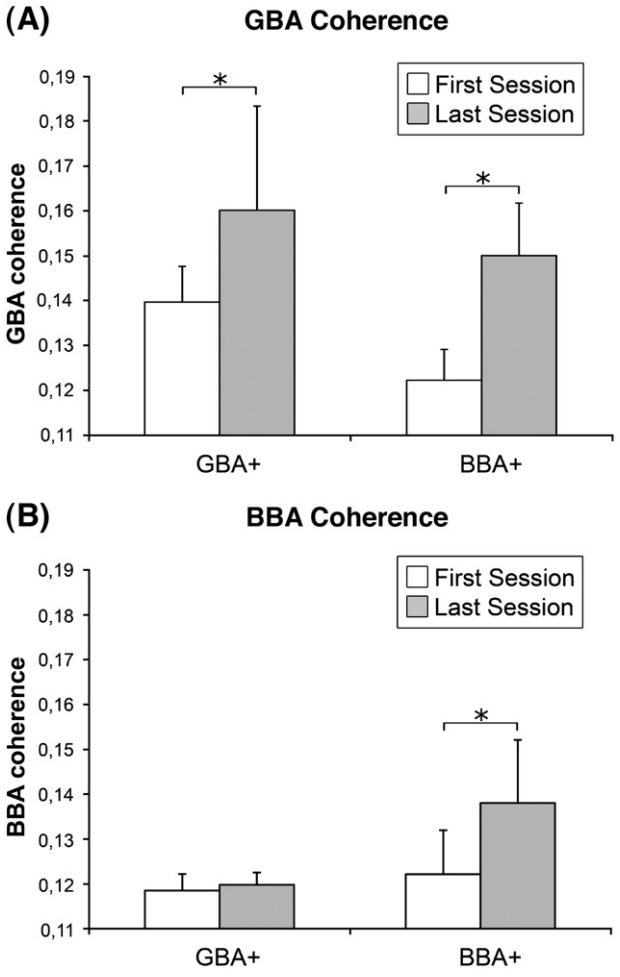

Fig. 4. Across sessions, the neurofeedback training resulted in a significant increase in GBA coherence in both groups (A) and a significant increase of BBA-coherence in the BBA+ group (B). Error bars represent standard errors, asterisks indicate significance level of $p<.05$.

Error rates of the pretest partially mirrored the reaction times results. There was a significant main effect of repetition/alternation of shape, $F(1,15)=7.1$, $p<.05$. Moreover, there was a significant interaction between the repetition/alternation of location and response, $F(2,15)=8.1$, $p<.05$ and between the repetition/alternation of shape and response, $F(1,15)=5.0$, $p<.05$. There were no significant interactions between any of the within subjects factors and the between subjects factor for both reaction times and error rates (p's>.09), indicating that the performance of both groups was similar on the pretest.

Individual binding costs were calculated by subtracting the mean reaction times and error percentages for the complete repetition condition and the complete alternation condition from the means of both partial repetition conditions[1], for both the pretest and posttest. This generated three measures that reflected binding between shape and location (Shape–Location), between location and response (Location–Response) and between shape and response (Shape–Response). In order to test the impact of neurofeedback training on

[1] The shape-location reaction time binding cost can be calculated using the following equation: $(RT_{\text{shape rep, location alt}} + RT_{\text{shape alt, location rep}})/2 - (RT_{\text{shape rep, location rep}} + RT_{\text{shape alt, location alt}})/2$. This represents the interaction term, which is not influenced by additive effects of shape and location repetition but as the interaction grows, the result of this equation increases as well.

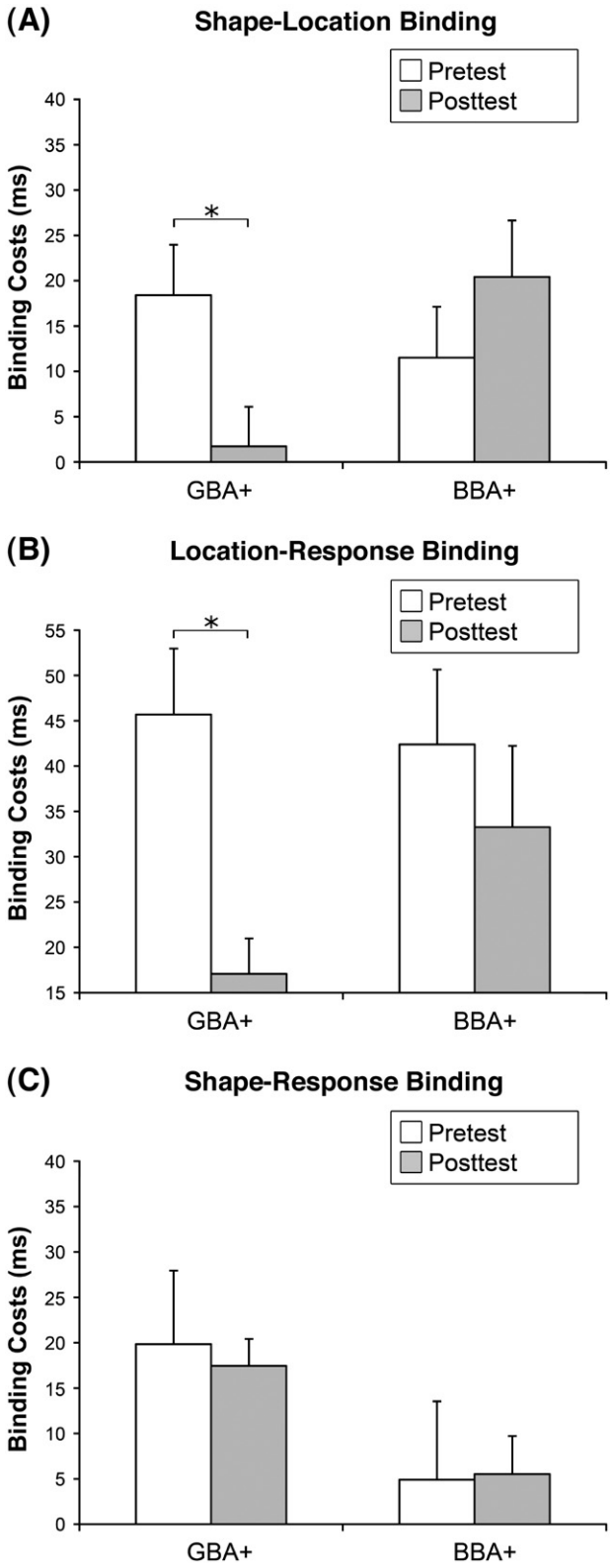

Fig. 5. Reaction time data of the binding task. The neurofeedback training resulted in a decrease of binding costs between shape and location (A) and between location and response (B), but not between shape and response (C). Error bars represent standard errors, asterisk indicates significance level of $p<.05$.

binding, we used three independent repeated measures ANOVAs with test instance (pretest versus posttest) as a 2-level within-subjects factor and group (GBA+ versus BBA+) as a between subjects factor we found a significant interaction between Shape–Location and group, $F(2,15)=4.9$, $p<.05$ (Fig. 5A). Post-hoc comparisons showed that this interaction is most likely to originate from a decrease in shape–location binding costs in the GBA+ group, $p=.065$. Second, we found a marginal significant interaction between Location–Response and group, $F(2,15)=4.1$, $p=.06$ (Fig. 5B). Post-hoc comparisons showed that this interaction is driven by a significant decrease of location–response binding costs in the GBA+ group, $p<.001$. Finally, there was no significant interaction between Shape–Response and group, $F(2,15)=.05$, $p>.8$ (Fig. 5C).

The error rates revealed only one reliable finding, an interaction between Shape–Response and group, $F(2,15)=5.3$, $p<.05$. Numerically, binding costs decreased from pre- to post-test in the GBA+ group (4.1% to 1.0%) and increased from pre- to post-test in the BBA+ group (0.5% to 3.7%). However, given that post-hoc comparisons did not render any of these changes significant, $p>.1$, the interaction is difficult to interpret.

Long-term memory

Performance on the study block was very good (mean error rate: 85%), indicating that subjects were able to discriminate between the colors of the drawings. Using a repeated measures ANCOVA with test instance (pretest versus posttest), percentage correct of remember versus know responses as within subjects factors and group (GBA+ versus BBA+) as a between subjects factor, we found no significant interaction between test instance, remember/know and group, $F(2,14)=3.4$, $p>.05$. To study the effects of neurofeedback on the more objective measure of familiarity and recollection, we used a repeated measures ANOVA with test instances (pretest versus posttest) and percentage correct of old–new responses (combined over remember/know responses) versus color retrieval responses as within subjects factors and group (GBA+ versus BBA+) as a between subjects factor. We found a significant main effect of test instance, $F(2,14)=8.3$, $p<.05$ which reflects a general increase of performance on the second test instance. A second main effect was found for the error rates of old–new responses versus color retrieval responses, $F(2,14)=24.2$, $p<.0005$, reflecting larger error rates for color retrieval responses. More importantly, we obtained a significant three-way interaction between test instance, old–new distinction versus color retrieval and group, $F(2,14)=8.8$, $p=.01$ (Fig. 6). Post-hoc planned comparisons revealed that this interaction was mainly driven by a significant increase of performance on color retrieval (recollection) in the GBA+

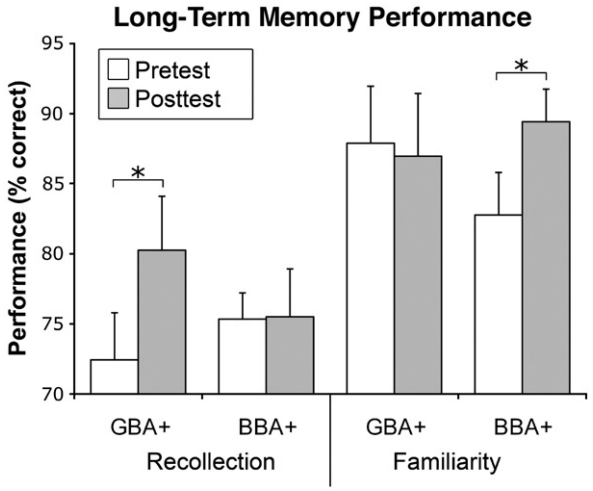

Fig. 6. The effect of enhanced GBA on LTM. Subjects in the GBA+ group showed a significant increase of performance on retrieval of the color (recollection), while the BBA+ group showed a significant increase of performance on the old–new discrimination (familiarity). Error bars represent standard errors, asterisks indicate significance level of $p<.05$.

group, $p<.005$, and a significant increase of performance on the old–new distinction (familiarity) in the BBA+ group, $p<.005$.

Discussion

Previous research suggests that GBA may play a role in feature integration and/or the management of integrated feature bindings. In the current study we tried to manipulate local GBA and BBA by means of neurofeedback, to further investigate and characterize the functional role of neural synchronization in short-term and longer-term feature binding, i.e., episodic LTM. Our results show that subjects were able to learn to increase occipital and frontal GBA through GBA-targeted neurofeedback and to increase BBA-based coherence between frontal and occipital areas through BBA-targeted neurofeedback. Subjects were able to increase occipital GBA, within sessions and across session. Frontal GBA was only increased across sessions These results are a direct replication of our previous neurofeedback study (Keizer et al., in press).

GBA-coherence between frontal and occipital electrode sites increased significantly in both learning groups and this change was already established in the first neurofeedback session. This does not only suggest that GBA-coherence is very sensitive to neurofeedback manipulations, but also that neural coherence is a means to transfer control signals. Indeed, a recent MEG study provided evidence that frontal areas use neural coherence to prepare upstream areas involved in stimulus processing for anticipated perceptual events (Gross et al., 2006). The idea that inter-area communication and control is mediated by neural coherence fits also with our findings from the BBA+ group. Even though this group showed no evidence of local BBA learning, it did show an increase in BBA-based coherence between frontal and occipital areas—which was not present in the GBA+ group. The feedback that these subjects received was dependent on BBA measured from both electrodes, suggesting that this type of feedback is functional in facilitating long-range neural communication. However, we need to be careful in interpreting our EEG findings, since we only measured the effects of neurofeedback training on two electrodes; Oz and Fz. This precludes definite conclusions regarding the location-specificity of the effects on local synchrony or regarding the specificity of the long-range coherence between Oz and Fz.

One might argue that the increase of GBA on Oz and Fz was not a result of increases in local neural synchrony in those regions but, rather, due to an increase in the number of neurons firing in the gamma frequency band. However, the available research favors the former over the latter interpretation. First, it has been demonstrated that the LFP amplitude in a particular frequency band is associated with neural synchronization in that frequency band (Eckhorn et al., 1993; Gray and Singer, 1989; Fries et al., 2001; Siegel and König, 2003). More specifically, it has been demonstrated that gamma power is directly dependent on neural synchrony (Herculano-Houzel et al., 1999). Second, it has been argued that asynchronous neural firing within a particular frequency band can only marginally contribute to frequency-specific EEG power, in stark contrast to synchronous neural firing (Taylor et al., 2005). Finally, increases in the rate of asynchronously firing neurons only leads to a frequency-unspecific increase of EEG power (Britten et al., 1993; Bair et al., 1994; Shah et al., 2004).

Interestingly, the neurofeedback training also affected performance on the behavioral tasks. First, we found a significant decrease of binding costs between shape and location and between location and response in the GBA+ group. This pattern has a number of interesting implications. For one, it does not suggest that our neurofeedback manipulation affected feature-integration processes proper. If feedback would have enhanced neural activities that are involved in integration, one would have expected more evidence of integration but not less, that is, an increase of binding costs and not a reduction. This does not necessarily rule out that gamma-band synchronization plays a role in the feature integration (Engel and Singer, 2001), but the method we used does not seem to tap into such processes. Our findings rather suggest that GBA feedback enhanced processes that handle already integrated bindings. Note that significant feedback effects were obtained for bindings that involved task-irrelevant features (location) but not for the binding that relates the two task-relevant aspects, shape and response (see Fig. 5). Apparently, GBA feedback reduced the impact of task-irrelevant feature bindings on performance (as in Keizer et al., in press), suggesting that this feedback enhanced the control and management of bindings in the suppression of irrelevant bindings in particular. An alternative explanation for the decrease in binding costs could be that the encoding, rather than the retrieval, of relational information is selectively reduced or impaired by enhanced GBA. Even though the design of our study does not allow ruling out an encoding interpretation entirely, previous demonstrations that the encoding of bindings is highly automatic and unimpaired by attentional load (e.g., Hommel, 2005) makes a retrieval-control account more plausible.

Second, we used an LTM paradigm that allowed us to distinguish between recollection and familiarity, the two dissociable processes that underlie recognition memory. The results of previous research are ambiguous regarding the role of GBA in these processes. On the one hand, the study of Burgess and Ali (2002) suggests that GBA is important for recollection but not for familiarity. On the other hand, a study of Gruber et al. (2008) suggests that GBA is important for familiarity, but not for recollection. Our experiment provides strong support for the first hypothesis: the results of the LTM task show a clear double dissociation between the two neurofeedback groups and the two types of recognition memory. Subjects in the GBA+ group significantly increased their ability to retrieve the color of the drawings in the retrieval phase that was presented during the encoding phase; an ability that is known to reflect recollection processes. Moreover, there was a significant positive correlation between the percent change in frontal GBA and the percent change of recollection. In contrast, the BBA+ group showed a significant increase in the ability to discriminate between 'old' and 'new' items, that is, between items that were previously presented during the encoding phase and items that were presented for the first time during the retrieval phase, which known to reflect familiarity processes. Since the BBA+ group showed an increase of BBA-coherence, but not of BBA power, the increase of familiarity must be attributed to the increase of BBA-coherence between frontal and occipital BBA in the BBA+ group. This conclusion fits with the findings of Sehatpour et al. (2008), which showed that object recognition was related to long-range beta coherence between the lateral occipital cortex (LOC), the hippocampus and prefrontal regions. In summary, our results clearly show that GBA is important for recollection, and that BBA-coherence between frontal and occipital brain areas is important for familiarity.

As with the effect of enhanced GBA on feature binding, the enhanced GBA may have either affected encoding or retrieval of relational information, or both. However, the selectivity of the effects of enhanced GBA on task-irrelevant bindings and the already mentioned evidence that binding encoding is strongly automatic (Hommel, 2005) suggest that the effects of enhanced GBA on recollection performance also reflect enhanced cognitive control.

It has been shown that recollection and familiarity depend on different brain areas. While recollection has been associated with the hippocampus and frontal–medial brain areas, familiarity seems to depend on the perirhinal cortex and lateral frontal areas (Yonelinas et al., 2005). Whereas the hippocampus is thought to be important for storing information, frontal brain areas have suggested to be related to higher-level retrieval-related mnemonic operations, such as organization, strategic search, monitoring and verification (Simons andpiers, 2003). In short, frontal brain areas seem to be important for the top–down control of memory traces which are stored in the hippocampus. Moreover, it has been shown that top–down processes

enhance GBA in occipital brain regions during visual attention (see for an overview: Engel et al., 2001). It can therefore be speculated that frontal brain areas may be the origin of the effects of GBA-enhancing neurofeedback, both in the EEG data and in the behavioural results. In contrast, the increased BBA-coherence between frontal and occipital brain areas in the BBA+ may reflect a rather control-free mechanism based on long-range communication in the beta range that underlies familiarity. Moreover, it can be hypothesized that the increase of BBA-coherence between frontal and occipital BBA in the BBA+ group reflects enhanced communication between visual brain areas in the occipital lobe and control related brain areas in the frontal lobe. This could result in facilitation of matching incoming visual representations with stored representations, which would enhance familiarity performance.

Conclusion

Taken together, our study demonstrates that neurofeedback can be a powerful tool in research on the functional relevance of neural synchrony in cognitive processes. The findings suggest that enhanced GBA allows for a greater flexibility in handling integrated information in short-term and long-term memory. In contrast, enhanced long-range communication in the beta range seemed to result in facilitation of familiarity-based processes. In both tasks, enhanced frontal GBA seems to have resulted in facilitated top–down control processes that affected the way memory traces of integrated information are organized and controlled. Apart from the important theoretical implications of these findings, the possibility that GBA-targeted neurofeedback can enhance memory control raises interesting questions regarding applicability. For instance, aging is known to hamper the control of memory retrieval (Reuter-Lorenz, 2002) and it would be interesting to see whether such deficits could be encountered by means of neurofeedback.

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